

Effects of Orchard Host Plants (Apple and Peach) on Development of Oriental Fruit Moth (Lepidoptera: Tortricidae)

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ABSTRACT Studies were designed to examine the effects of host plants (apple, *Malus domestica* Borkh., and peach, *Prunus persica* L.) on the development of oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae). Oriental fruit moth larvae developed faster on peach than on apple, both on fruit as well as on growing terminal shoots. On fruit, these differences were shown to cause significant changes in both the rate (≈ 20 –60 degree-days earlier emergence on peach than on apple) and patterns of adult emergence among several cultivars of peaches and apples. Slopes of female emergence plots varied by host in 2003, with emergence occurring over a longer period on peach cultivars than on apple cultivars (with one exception). Slopes of male emergence curves did not differ by cultivar in 2003. These host-driven effects could impact the efficacy of traditional pest management approaches and probably complicate efforts to predictively model *G. molesta* populations in mixed cultivar orchards. Such developmental effects may help to explain previously observed differences in patterns of pheromone trap captures in peach versus apple orchards. Host-associated effects should be incorporated into future models to develop more realistic predictive tools and thus improve integrated pest management efforts.

KEY WORDS oriental fruit moth, developmental rate, apple, peach, population dynamics

Herbivore–host plant interactions can have an important influence on the dynamics and management of pest populations. For Oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae), a deciduous tree fruit pest species of key importance in the eastern United States, multiple tree fruit crops, including stone fruits and apple (*Malus* spp.), serve as suitable host plants. Although historically *G. molesta* has primarily been considered a stone fruit pest, and only a minor pest of concern on apples, recent outbreaks in commercial apple orchards have become prevalent in the mid-Atlantic region. The reasons for recent population outbreaks are unknown.

Host plant effects on *G. molesta* may contribute to changes in orchard population dynamics. Host-associated races have been identified among related tortricid pests, including the codling moth, *Cydia pomonella* (L.) (Cisneros and Barnes 1974), and fruit-tree leafroller, *Archips argyrospila* (Walker) (Goyer et al. 1995). The host association status of eastern *G. molesta* populations is unknown. Preliminary evidence suggests that most populations are probably not genetically distinct races, but rather may be “ectomorphs” (Pashley 1993), where various populations are affected differentially by their respective host

plants (Myers 2005; C.T.M. et al., unpublished data). Oriental fruit moth larvae feed at different sites on peaches (*Prunus* spp.) and apples over the course of the growing season, and this feeding behavior has been well described (Garman 1918, Frost 1930, Peterson and Haeussler 1930, Allen 1958, Phillips and Proctor 1969, Reichart and Bodor 1972, Yokoyama and Miller 1988, Rothschild and Vickers 1991). Adult ovipositional behavior (Myers et al. 2006b,c) is affected by host plant, as well as larval developmental rate on fruit (Peterson and Haeussler 1928) and reproductive output (Myers et al. 2006a).

Oriental fruit moth larvae complete four to five instars (Peterson and Haeussler 1928, Roberts et al. 1978, Russel and Bouzouane 1989). Using Dyar’s rule (Dyar 1890), instars of lepidopteran larvae can be identified based on their head capsule widths, which fall within discrete boundaries for each instar. Although temperature can affect individual head capsule widths, Dyar’s head capsule–instar relationship has been validated for identification of *G. molesta* instars (Roberts et al. 1978, Russel and Bouzouane 1989). Dyar’s relationship was previously used by Peterson and Haeussler (1928) to classify instars and to show a difference in larval developmental rates on peach and apple fruit. However, it is unknown how this difference translates to patterns of adult emergence over time and whether developmental effects vary at the cultivar level for peach and apple fruit. Also, no previous reports have described how devel-

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opmental rate of *G. molesta* is affected by feeding on shoots.

Other tortricid pests, including *Choristoneura rosaceana* (Harris) (Onstad et al. 1986) and codling moth (Riedl et al. 1998, Bezemer and Mills 2001; Hansen et al. 2002, 2004) are known to exhibit differential rates of larval survival and development, depending upon host plant food source. Any of the aforementioned developmental effects could significantly impact *G. molesta* population dynamics in ways that are not taken into account by current peach-based developmental models (Hull et al. 2001). Thus, a series of studies were designed to address the following hypotheses: 1) *G. molesta* larval development, adult emergence, and longevity are affected by peach and apple fruit and may vary by cultivar; and 2) the developmental rate of *G. molesta* larvae differs on peach and apple shoots.

Materials and Methods

Insects. *G. molesta* larvae used in the studies were from a colony maintained at The Pennsylvania State University Fruit Research and Extension Center, Biglerville, PA. Founder individuals for this colony were collected from infested peach (*Prunus persica* L.) and apple (*Malus domestica* Borkh.) orchards along with larvae from infested apple and peach fruit rejected by local fruit processors during the 1997 and 1998 growing seasons. Larvae were transported to the laboratory, removed from plant material, and placed in plastic containers (36 by 72 cm) with $\approx 1,500$ ml of a meridic lima bean diet (Meagher 1985). These containers were maintained either in growth chambers or on countertop space in the laboratory at $\approx 22 \pm 2^\circ\text{C}$ on a photophase of 16:8 (L:D) h.

Cardboard strips (1–3 cm in width) were placed on top of the media in the feeding trays to provide sites for pupation. Pupae were then placed into rectangular, wood-framed mating chambers (≈ 30 by 42 by 12 cm) that were lined on one side with wax paper and provisioned with a 10% honey solution containing a cotton wick for adult feeding. After emergence, adults mated within the chambers and females oviposited on the wax paper lining. Wax sheets filled with 5,000–7,000 eggs were removed daily and placed in the containers with the lima bean diet. Larvae for all studies were taken from this colony.

Larval Development on Fruit, 2001–2004. For all larval developmental studies, the date of larval placement or release in the field was recorded and related to wild *G. molesta* phenology, based upon the outdoor accumulation of degree-days (DD) ($^\circ\text{C}$) past biofix (date of first sustained *G. molesta* male moth capture in a pheromone trap placed in a nearby orchard) (Hull et al. 2001). Although degree-days are not a measure of host plant phenology per se, the phenology of *G. molesta* does coincide with the development of host plants to an appreciable, predictable manner from year to year (i.e., first brood *G. molesta* encounter trees with very small fruit and ample succulent shoot growth, whereas later broods feed on fruit at varying

stages of development). Thus, expression of time in *G. molesta* degree-days provides some indication of the type of host plant conditions present for each study.

In 2001, *G. molesta* larvae were reared on excised fruit of peach ('Autumn Glo') and apple ('York Imperial') in a study that was started on 7 August. Fruit for the study were collected from trees not sprayed with insecticides. Average fruit diameter ranged from 4.0 to 5.0 cm and from 6.0 to 8.0 cm for apples and peaches, respectively. Fruit were washed with soap and warm water, rinsed, and allowed to air dry. Fruit were placed into clear plastic containers, ≈ 45 by 28 by 9.5 cm in height. Each container was filled with 70 apples or 70 peaches. Three neonates per fruit (<24 h old) were transferred to fruit containers by using a camel's-hair brush. Neonates were placed on the stem of peach fruit and on the calyx of apple.

Each container was capped with a plastic lid containing two screened 5- by 7-cm ventilation holes. Containers were placed in an outdoor screenhouse insectary. The insectary was ≈ 10 by 8 m, with block walls ≈ 1 m in height, supporting screen windows ≈ 1.5 m in height. The building was covered with a translucent corrugated plastic roof, which provided some degree of shading from ambient sunlight. Temperature conditions in the insectary were very comparable to conditions outside, but experiments were sheltered from wind and precipitation. Temperature was monitored with an on site weather station, which was located ≈ 50 m from the insectary. Accumulated degree-days were calculated using daily maximum and minimum temperatures beginning with the day of initial larval placement, by using an established *G. molesta* developmental model, base 7.2°C , maximum 32.2°C (Hull et al. 2001). As prepupae started to occur within the containers, small, corrugated paper strips were placed within each to provide sites for pupation. Adult emergence was tracked daily, and adults were separated and categorized by sex. Adults were collected from the containers by using an aspirator. Adults were sexed and placed individually into 30-ml plastic cups to prevent mating with other individuals. Mean emergence time, calculated as the accumulated degree-days from neonate placement to adult emergence, was tabulated for each individual on both peaches and apples, and means were compared using an unpaired *t*-test ($P < 0.05$) (Minitab, Inc. 2000).

In 2003 and 2004, the study was repeated using similar methods, except that multiple cultivars of apples and peaches were examined. In 2003, feeding containers were set up on 7 July (70 fruit and 210 larvae per tray) with Autumn Glo and 'Redhaven' peaches, as well as 'Delicious,' 'Golden Delicious,' and York Imperial apples. Two containers were established for each cultivar (i.e., 140 fruit and 420 larvae per treatment). Adult emergence was tracked for each host. Adults were stored individually in plastic 30-ml cups, which were each provisioned with a moist cotton ball. Adults remained in the insectary under ambient temperature conditions. Cotton balls were replenished with water daily, and moth mortality was assessed daily. Emergence time and moth longevity

were calculated for each adult. Differences in both variables were analyzed using a one-way analysis of variance (ANOVA), and means were separated using Tukey's test ($P < 0.05$) (Minitab, Inc. 2000).

In 2004, a 'Sun Glo' nectarine treatment was added to the study. Two feeding containers were established for each cultivar treatment on 28 June, but only one container for each treatment was used to track adult emergence. The second container was used for sampling larvae for periodic head capsule measurements (described below). Differences in emergence time were analyzed using a one-way ANOVA, and means were separated using Tukey's test ($P < 0.05$) (Minitab, Inc. 2000). Adult longevity was not measured in 2004.

For all emergence data (2001, 2003–2004), cumulative adult emergence curves over time (accumulated degree-days, °C) were constructed. Because cumulative emergence curves were sigmoidal, all data were transformed using the inverse cumulative normal distribution function (Minitab, Inc. 2000). This function transformed the sigmoidal proportion data to a linear relationship with time, relating the data to a normal distribution of -3 (for zero) through 3 (for 1), with 0.5 cumulative emergence set equal to zero (the mean of a normal distribution). Linear regression analysis was conducted on the transformed cumulative emergence data versus cumulative degree-days (°C). To make pairwise comparisons of regression slopes, t values were calculated using the following equation:

$$T = \frac{(m_1 - m_2) - \mu_{m_1 - m_2}}{\text{Sqrt}([\text{SE}_{m_1}]^2 + [\text{SE}_{m_2}]^2)}$$

where T is t value, m_1 is slope of regression line 1, m_2 is slope of regression line 2, $\mu_{m_1 - m_2}$ is the hypothesized difference in slopes (H_0 is no difference, so $\mu_{m_1 - m_2} = 0$), SE_{m_1} is standard error of regression slope 1, and SE_{m_2} is standard error of regression slope 2. P values were derived from a T distribution (Zar 1999). Slopes were considered significantly different if $P < 0.05$.

In 2004, larval developmental studies were conducted simultaneously with adult emergence studies. Neonate larvae were placed in previously described containers (70 fruit, 210 larvae per cultivar of each host) and were destructively sampled 7 d (112 DD) after initial placement. Thirty fruit from each container were collected and examined for the presence of live larvae. Live *G. molesta* larvae were collected and placed by cultivar into plastic, capped 30-ml cups, and subsequently killed by placement in a freezer (temperature $< -10^\circ\text{C}$). Larvae were stored in the freezer until head capsule measurements could be taken. Head capsule width measurements were made using a stereomicroscope at 20–30 \times magnification.

Although wild populations of *G. molesta* can sometimes undergo five instars (Peterson and Haeussler 1928, Roberts et al. 1978), four instars were assumed for this laboratory reared population and instars were determined using criteria described by Roberts et al. (1978). Larvae with head capsule width $< 210\ \mu\text{m}$

were classified as first instars. Head capsules larger than $270\ \mu\text{m}$ but smaller than $400\ \mu\text{m}$ were second instars, those larger than $485\ \mu\text{m}$ but smaller than $715\ \mu\text{m}$ were third instars, and those larger than $800\ \mu\text{m}$ were classified as fourth and older instars. Larvae with head capsule widths between the given discrete values were rounded up or down to the nearest instar classification. For each cultivar, the proportion of total larvae in each instar was calculated. Due to low larval survival in some cultivars, instar distributions were pooled by host (i.e., all peach versus all apple). Proportions of larvae placed in each instar were compared between hosts using a Z test ($P < 0.05$) (Minitab, Inc. 2000).

Larval Development on Shoots, 2002–2003. Larval developmental studies were conducted on growing shoots of young, nonbearing peach and apple trees. Trees were planted in March 2001, and they were heavily fertilized to induce rapid shoot growth in the first season. Apple trees were York Imperial on 'Malling Merton' (MM) 111' rootstock. Peach trees were 'Loring' on 'Lovell' rootstock. Trees were planted in rows by species, at a spacing of ≈ 2.5 by 5 m. Trees were pruned annually and treated with a regular schedule of fungicides to prevent disease development in all years. Trees also were treated with insecticides (phosmet, azinphosmethyl, methomyl, and imidacloprid) periodically to prevent infestation from wild populations of arthropod pests. Trees used for bioassays were not treated with insecticides within 14 d of use.

Trees used for developmental studies were covered with wood framed, mesh cages. Cages were ≈ 1.5 m in height and 1 by 1 m in length and width. Trees were accessible from the top of the cage by opening a mesh door sealed to the cage with Velcro tape. Cages were anchored with clothesline tied to 2-m iron stakes, which were driven into the ground on lateral sides of each cage. On each shoot (range, of 20–70 shoots per tree), three neonate *G. molesta* larvae were placed with a camel's-hair brush to compensate for anticipated high levels of larval mortality (Wylie 1966, Philips and Proctor 1969). Five to 10 trees of each species were used for each study, depending on tree availability, and 20–70 growing shoots were used on each tree, depending on tree growth and shoot availability. All larvae for these studies were taken from the colony as described previously. After the accumulation of 110–130 DD after larval infestation, trees were examined for the presence of *G. molesta* damage. At the time of sampling, all visible shoot damage was clipped and taken back to the laboratory for recovery of larvae. Live *G. molesta* larvae were collected and placed by host into plastic, capped 30-ml cups, and killed by placement in a freezer. Head capsule measurements, instar determination protocols, and analyses of instar distributions were the same as described previously.

Results

Larval Development on Fruit, 2001–2004. Transformation of adult emergence curve data from larval studies conducted in 2001 and 2003–2004 resulted in

Table 1. Linear regression analyses for emergence of male and female oriental fruit moth adults over time from fruit of various peach and apple cultivars, 2001, 2003–2004

Yr	Cultivar	Sex	Regression statistics—summary					
			Slope	SE slope	R ² adj	df	F value	P value
2001	Autumn Glo	♀	0.0211	0.0025	81.8	15	72.68	<0.001
	York Imperial	♀	0.0345	0.0027	94.3	9	167.84	<0.001
	Autumn Glo	♂	0.0279	0.0012	97.6	12	522.19	<0.001
	York Imperial	♂	0.0369	0.0041	89.9	8	81.5	<0.001
2003	Autumn Glo	♀	0.0043	0.0004	88.2	14	113.62	<0.001
	Redhaven	♀	0.0094	0.0009	86.3	16	107.91	<0.001
	Delicious	♀	0.0106	0.0019	87.5	9	70.85	<0.001
	Golden Delicious	♀	0.0238	0.0030	84.1	11	64.32	<0.001
	York Imperial	♀	0.0276	0.0028	89.5	10	94.81	<0.001
	Autumn Glo	♂	0.0227	0.0020	91.4	11	128.43	<0.001
	Redhaven	♂	0.0281	0.0023	92.9	10	144.61	<0.001
	Delicious	♂	0.0221	0.0023	86.7	14	98.61	<0.001
	Golden Delicious	♂	0.0218	0.0028	82.1	12	60.69	<0.001
	York Imperial	♂	0.0254	0.0029	85.7	12	79.06	<0.001
	Autumn Glo	♀	0.0442	0.0026	97.3	7	194.69	<0.001
	Redhaven	♀	0.0602	0.0039	97.6	5	244.73	<0.001
2004	Sun Glo	♀	0.0311	0.0014	97.5	11	470.52	<0.001
	Delicious	♀	0.0370	0.0025	96.0	8	215.15	<0.001
	Golden Delicious	♀	0.0228	0.0034	77.6	12	46.10	<0.001
	York Imperial	♀	0.0363	0.0032	93.5	8	131.25	<0.001
	Autumn Glo	♂	0.0332	0.0024	95.1	9	194.63	<0.001
	Redhaven	♂	0.0396	0.0040	92.3	7	96.71	<0.001
	Sun Glo	♂	0.0277	0.0017	95.5	12	278.02	<0.001
	Delicious	♂	0.0485	0.0037	96.0	6	167.19	<0.001
	Golden Delicious	♂	0.0333	0.0035	90.0	9	90.70	<0.001
	York Imperial	♂	0.0431	0.0044	92.4	7	97.68	<0.001

Emergence data transformed using the inverse normal cumulative distribution with three standard deviation units (Minitab, Inc. 2000).

highly significant linear relationships between time (accumulated degree-days) and cumulative emergence for all cultivars within both host species. This was true for both moth sexes and for every cultivar tested from 2001 to 2004 (Table 1).

Plots of both female and male emergence in 2001 indicated that development occurred faster on peach compared with apple fruit (Fig. 1). Moreover, mean emergence time for females developing on peach fruit (446.8 ± 3.9 DD) was significantly less than females developing on apple fruit (469.7 ± 5.4 DD) ($T = -3.43$, $df = 62$, $P = 0.001$). Similarly, males reared on peach (421.3 ± 4.6 DD) emerged earlier than males reared on apple (456.1 ± 5.1 DD) ($T = -5.06$, $df = 74$, $P < 0.001$). Protandrous emergence was significant for peach-reared individuals ($T = -4.20$, $df = 106$, $P < 0.001$) but not apple-reared individuals ($T = 1.84$, $df = 61$, $P = 0.071$). The slope of the transformed emergence curve for females on peaches was flatter than the slopes of emergence curves from both males emerging from peaches and from females emerging from apples (Table 2). The slope of the transformed emergence data for males developing on peach fruit was flatter than that for males emerging from apple fruit (Table 2).

In 2003, mean emergence time varied significantly by cultivar for both female ($F = 21.61$; $df = 4, 578$; $P < 0.001$) and male ($F = 16.29$; $df = 4, 559$; $P = 0.001$) adults. Female emergence was the most rapid on Redhaven peaches (392.2 DD). Female emergence on Autumn Glo (417.0 DD) peach was similar to Golden Delicious (425.8 DD) and York Imperial (427.3 DD) apples but was significantly earlier than Delicious

(441.3 DD) (Fig. 2A). Female emergence from Golden Delicious (425.8 DD) and York Imperial (417.0 DD) was more rapid than emergence from Delicious (441.3 DD) apples. Male emergence varied among cultivars in a similar manner, except that male emergence on Autumn Glo (401.6 DD) peach was similar to all three apple cultivars (Fig. 2A). Male moths emerged significantly earlier than female moths in four of the five evaluated cultivars (Autumn Glo, $T = 1.31$, $P = 0.190$; Redhaven, $T = 2.14$, $P = 0.034$;

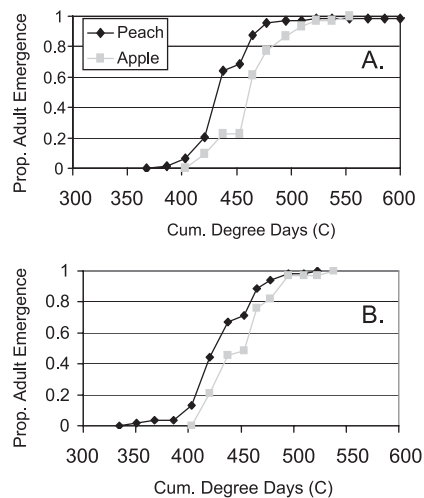


Fig. 1. *G. molesta* female (A) and male (B) emergence from Autumn Glo peach and York Imperial apple fruit after feeding as larvae in 2001.

Table 2. Comparison of slopes of *G. molesta* adult emergence from Autumn Glo peach and York Imperial apple fruit by sex and by host, 2001

Host	Sex	Slope	T and P values for pairwise slope comparisons ^a			
			Peach ♀ m ^b = 0.0211	Apple ♀ m = 0.0345	Peach ♂ m = 0.0279	Apple ♂ m = 0.0369
Peach	♀	0.0211				
Apple	♀	0.0345	-3.70, 0.001			
Peach	♂	0.0279	-2.46, 0.020			
Apple	♂	0.0369		-0.49, 0.628	-2.11, 0.048	

^a Slopes compared using *t*-test (Zar 1999).
^b m is slope for regression equation.

Golden Delicious, $T = 4.61$, $P < 0.001$; Delicious, $T = 6.46$, $P < 0.001$; and York Imperial, $T = 5.80$, $P < 0.001$) (Fig. 2A).

When emergence data were transformed into straight lines, slope values varied by host and cultivar within host for females, indicating that the length of the emergence period was longer on peach relative to apple (Table 3). Slope values for male emergence did not vary between hosts or among cultivars (Table 3). Moth longevity varied by host for males ($F = 13.48$; $df = 4, 496$; $P < 0.001$), but there were no significant differences among cultivars within either host (Fig.

3). Among females, a similar trend was observed, except that longevity of moths reared on Redhaven was not significantly different from that observed on the apple cultivars (Fig. 3).

In 2004, emergence time also varied significantly by host and cultivar for both female ($F = 31.96$; $df = 5, 257$; $P < 0.001$) and male ($F = 21.00$; $df = 5, 259$; $P = 0.001$) adults. In peaches, female emergence was most rapid on Autumn Glo (398.3 DD) and Redhaven (407.7 DD), with Autumn Glo emergence occurring significantly faster than emergence from Sun Glo (416.4 DD) (Fig. 2B). When comparing hosts, female emergence was more rapid for all three peach cultivars than for Delicious (452.0 DD) or York Imperial (460.0 DD) apples, but it was not different from Golden Delicious (426.2 DD) apples. Female emergence from Golden Delicious was more rapid than emergence from Delicious and York Imperial apples. Male emergence varied between hosts and cultivars in a similar manner (Fig. 2B), except there was no difference in emergence time between any of the peach cultivars. Male moths emerged significantly earlier than female moths in all six cultivars (Autumn Glo: $T = 2.29$, $P = 0.026$; Redhaven: $T = 3.48$, $P = 0.001$; Sun Glo: $T = 3.38$, $P = 0.001$; Golden Delicious: $T = 2.87$, $P = 0.005$; Delicious: $T = 3.91$, $P < 0.001$; and York Imperial: $T = 5.52$, $P < 0.001$) (Fig. 2B).

When emergence data were transformed, slope values varied between hosts and among several cultivars within hosts for both females and males (Table 4). In females, the slope of York Imperial apple emergence differed from Redhaven peach and Golden Delicious apple, whereas the slope of Delicious differed from Redhaven, Sun Glo, and Golden Delicious. In males, the slope of Delicious emergence was significantly steeper than slopes from Autumn Glo, Sun Glo, or Golden Delicious. The emergence slopes of Redhaven and York Imperial were both significantly steeper than the slope for Sun Glo (Table 4).

In 2004, when *G. molesta* larvae were sampled from host fruit 112 DD postneonate placement, instar distributions seemed to vary numerically between hosts, among three peach cultivars and three apple cultivars. When larval samples were pooled by host plant (i.e., all peach cultivars pooled and all apple cultivars pooled), the proportion of second and fourth instars differed significantly between peach and apple fruit (Table 5). Second instars were only present in apple

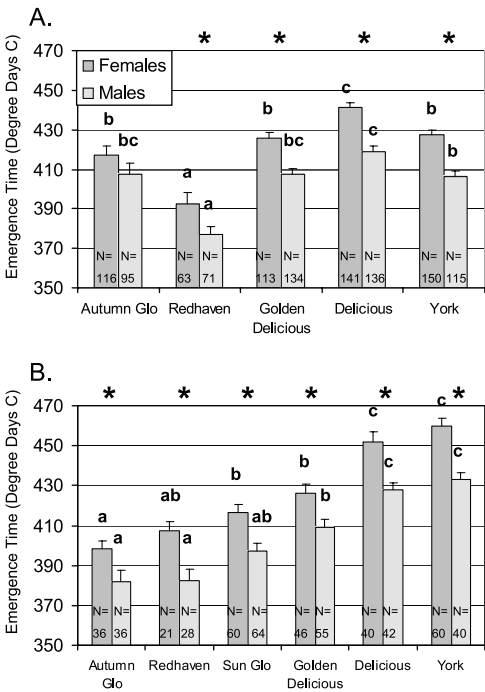


Fig. 2. Mean \pm SEM time of adult emergence (in degree-days) of *G. molesta* cohorts reared on various cultivars of peach and apple fruit after infestation with neonates on 7 July 2003 [858 degree-days °C postbiofix] (A) and on 28 June 2004 [827 degree-days °C postbiofix] (B). Means within each sex with the same letter are not significantly different (Tukey's test; $P < 0.05$). Paired means within each cultivar (i.e., female mean versus male mean for each cultivar) marked with an asterisk are significantly different (unpaired *t*-test; $P < 0.05$). *n* = number of emerged adults for each group.

Table 4. Comparison of slopes of female and male moth emergence (inverse normal cumulative distributions) by host fruit and cultivar, 2004

Sex	Cultivar	Slope	T and P values for pairwise slope comparisons ^a					
			Females			Males		
			Sun Glo m = 0.0311	Golden Del. m = 0.0228	Delicious m = 0.0370	York Imp. m = 0.0363	Autumn Glo m = 0.0332	Redhaven m = 0.0396
♂	Autumn Glo	0.0442						
♂	Redhaven	0.0602						
♂	Sun Glo	0.0311						
♂	Golden Del.	0.0228						
♂	Delicious	0.0370						
♂	York Imp.	0.0363						
♀	Autumn Glo	0.0332						
♀	Redhaven	0.0396						
♀	Sun Glo	0.0277						
♀	Golden Del.	0.0333						
♀	Delicious	0.0485						
♀	York Imp.	0.0431						

^a Slopes compared using *t*-test (Zar 1999).
^b *m* is slope for regression equation.

Table 5. Instar distribution of larvae reared on live fruit from three peach and three apple cultivars from 29 June through 6 July, 2004^a with pooled analysis of instar distributions between apples (all cultivars) and peaches (all cultivars)

Host	Instar	Instar distribution		Apple vs. peach comparison		
		<i>n</i>	Percentage	Instar comparison	Z value ^b	P value
Apple	2	4	13.3	2	2.15	0.032
	3	26	86.7	3	1.35	0.178
	4+	0	0.0	4+	3.84	<0.001
Peach	2	0	0.0			
	3	32	74.4			
	4+	11	25.6			

^a Release on fruit conducted on 29 June—891 degree-days (°C) postbiofix, larvae collected on 6 July—1003 degree-days (°C) post-biofix; 112 degree-days elapsed.
^b Zar 1999 and Minitab, Inc. 2000.

cultivars presently grown in the United States (especially true for *Malus* spp.), future studies should be conducted to compare development on a greater number of cultivars. It is possible that cultivar level variability could supercede host level variability if a larger and more diverse group of cultivars were tested. Cultivar level variation in *G. molesta* developmental time would probably add additional complexity to the population dynamics of *G. molesta* in mixed cultivar blocks, which are common, and well within the typical dispersal range of *G. molesta* adults (Yetter and Steiner 1931, 1932; Steiner and Yetter 1933; Hughes and Dorn 2002). Finally, consideration must be given to the cumulative effect of small developmental differences over the course of a season. Given that *G. molesta* is multivoltine, small host-driven differences in devel-

Table 6. Instar distribution of larvae reared on live peach and apple shoots for first release on 6 May 2002 and second release on 10 June 2002

Host	Instar	Instar distribution		Apple vs. peach comparison		
		<i>n</i>	%	Instar comparison	Z value ^c	<i>P</i> value
6 May ^a						
Apple	2	0	0.0	2		
	3	9	100.0	3	11.71	<0.001
	4+	0	0.0	4+	−11.71	<0.001
Peach	2	0	0.0			
	3	22	33.3			
	4+	45	66.7			
10 June ^b						
Apple	2	1	1.0	2	1.00	0.315
	3	40	36.3	3	5.90	<0.001
	4+	69	62.7	4+	−5.90	<0.001
Peach	2	0	0.0			
	3	3	4.9			
	4+	58	95.1			

^a Release 1 conducted on 6 May—203 degree-days (°C) postbiofix, larvae collected on 23 May—317 degree-days (°C) postbiofix; 114 degree-days elapsed.
^b Release 2 conducted on 10 June—560 degree-days (°C) postbiofix, larvae collected on 20 June—692 degree-days (°C) post biofix; 132 degree-days elapsed.
^c Zar 1999 and Minitab, Inc. 2000.

Table 7. Instar distribution of larvae reared on live peach and apple shoots for first release on 22 May 2003 and second release on 8 July 2003

Host	Instar	Instar distribution		Apple vs. peach comparison		
		<i>n</i>	%	Instar comparison	Z value ^c	<i>P</i> value
22 May ^a						
Apple	2	61	89.7	2	5.57	<0.001
	3	7	10.3	3	-4.96	<0.001
	4+	0	0.0	4+	-2.07	0.038
Peach	2	29	48.3			
	3	27	45.0			
	4+	4	6.7			
8 July ^b						
Apple	2	12	27.3	2	0.81	0.418
	3	32	72.7	3	3.42	0.001
	4+	0	0.0	4+	-5.05	<0.001
Peach	2	6	19.4			
	3	11	35.4			
	4+	14	45.2			

^a Release 1 conducted on 22 May—247 degree-days (°C) postbiofix, larvae collected on 4 June—359 degree-days (°C) postbiofix; 112 degree-days elapsed.

^b Release 2 conducted on 8 July—877 degree-days (°C) postbiofix, larvae collected on 16 July—996 degree-days (°C) postbiofix; 119 degree-days elapsed.

^c Zar 1999 and Minitab, Inc. 2000.

opmental rate could become very large when developmental differences manifest themselves over multiple generations. For example, if development of *G. molesta* is delayed by 50 DD on apples relative to peaches for a given generation, total delay of emergence may be close to 150 DD by the time the fourth brood population emerges late in the season.

Beyond developmental rate differences, interesting differences were observed in the patterns of emergence over time. Slopes of adult female emergence curves varied by host in 2003. Emergence occurred over a longer period on peach than on apple cultivars (except between Redhaven peaches and Delicious apples, which did not differ). This pattern is in agreement with data from 2001, where emergence of both males and females also occurred over a longer period on peach than apple. However, slopes of male emergence curves did not differ by cultivar in 2003, indicating essentially parallel emergence. Slope calculations for 2004 were more erratic due to much smaller sample sizes than 2003 (approximately half for each cultivar, because the study was split to accommodate a simultaneous sampling of larvae for head capsule measurements). Thus, comparisons between emergence slopes in 2004, as presented here, are probably less likely to be meaningful.

Adult females reared on apple fruit lived longer compared with those reared on Autumn Glo peach. Male adults lived longer on all apple cultivars compared with Autumn Glo or Redhaven peaches. Longer living males may be available to mate for a longer period in apples, thereby increasing opportunities for more multiple matings. Oriental fruit moth males were reported to mate up to seven times by Dustan (1964).

However, relative differences in longevity among female moths were much smaller, despite a statistically significant separation of mean longevity on Autumn Glo peaches from other apple cultivars.

Diet makeup and quality is well established as an important factor in the survival and development of related tortricid species. Codling moth larval survival and developmental rate were negatively affected by the presence of cherry (*Prunus* spp.) fruit in the diet (Hansen et al. 2004) with these effects varying among cherry cultivars (Hansen et al. 2002). Larval survival of codling moth varied among different apple cultivars, depending upon the developmental state of fruit (Riedl et al. 1998). In walnuts (*Juglans* spp.), codling moth larvae developed faster on early maturing versus later maturing cultivars (Bezemer and Mills 2001). In the obliquebanded leafroller, apple leaf quality affected larval survival and development (Onstad et al. 1986).

Interpretation and application of our data to wild *G. molesta* population dynamics may be somewhat limited due to the use of excised fruit. Fruit sugar levels and allelochemistry may be affected by fruit degradation, larval feeding, or excision from the tree. Future studies should assess developmental differences of larvae reared on live, growing fruit. However, data from excised fruit are of value for modeling populations of wild *G. molesta* that develop in fruit that has dropped from the tree, especially for *G. molesta* developing on fruit thinned early in the season, on fruit prematurely dropping from the tree (sometimes caused by *G. molesta* damage itself), or on harvested fruit. Depending on pest pressure and a number of other factors, a large portion of a given population may develop in such "excised" fruit. Thus, the effects observed in our studies may be relevant to wild *G. molesta* population dynamics.

This study also presents the first known report of differences in *G. molesta* larval developmental rate between peach and apple shoots. Differences in instar distributions for larvae reared from shoots were similar to those differences observed in fruit. The timing of larval sampling was similar on both plant parts, with samples taken ≈110–130 DD after placement of larvae on hosts. Indeed, timing of larval sampling on both plant parts may be critical to observing differences in developmental rate and head capsule sizes. Additional samples taken subsequent to initial larval samples from the same releases on shoots (in both 2002 and 2003) exhibited fewer differences in instar distributions between peach and apple. This result may have been due to the inability to determine the exact age of larvae within a given instar. Additionally, pupae were not sampled because pupation occurs outside of infested shoots (Stearns 1927, Allen 1958).

Additional studies in which *G. molesta* larvae were placed on the shoots of potted peach and apple trees in a screened outdoor insectary were undertaken in an effort to investigate development and adult emergence from shoots under ambient conditions. Larval survival was low and sample sizes of adults were never high enough to provide emergence plots of any rele-

vance. Thus, conclusions for larval development on shoots are based solely on head capsule measurement data. However, given the similarity of head capsule data from shoots and fruit, it seems reasonable to hypothesize that differences in larval developmental rates between peach and apple shoots are similar to those observed in fruit. For larvae reared on fruit in 2004, head capsule measurements taken 112 DD postinfestation indicated a significant difference in instar distributions. These larvae were sampled from the same population that later exhibited differences in mean emergence time between peaches and apples (with the exception of adults from Golden Delicious, which were similar to individuals reared on peach cultivars). Estimates of differences in developmental time for *G. molesta* from peach fruit compared with apple fruit would range from 20 to 60 DD, depending on the cultivar. We hypothesize that a similar difference in adult emergence time would result from populations reared on shoots, which showed a similar divergence in instar distribution at sampling times 110–130 DD postinfestation. Future studies are required to investigate this relationship and to more precisely quantify the differences in developmental rates between peach and apple shoots.

Host-driven differences in development could have important implications for modeling and managing *G. molesta* populations in areas where peach and apple are grown in proximity. Oriental fruit moth survival (Myers et al. 2006d), adult reproductive output (Myers et al. 2006a), and oviposition behavior (Myers et al. 2006b,c) also are affected by host. Sex pheromone trap capture and egg hatch data (L.A.H. and C.T.M., unpublished data) of *G. molesta* populations in south central Pennsylvania indicate a great amount of developmental/generational overlap of *G. molesta* populations in apple blocks, especially from July through September. This is in contrast to more distinct periods of adult male flight and egg hatch phenology among broods in peach blocks (L.A.H. and C.T.M., unpublished data). Given the extent to which host plants seem to affect *G. molesta* biology, it is reasonable to hypothesize that such host effects are a significant contributor to these observed phenomena.

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